



Burrows, M., Cullen, D., Doroshenko, M., & Sutton, G. P. (2015). Mantises Exchange Angular Momentum between Three Rotating Body Parts to Jump Precisely to Targets. *Current Biology*, 25(6), 786-789. <https://doi.org/10.1016/j.cub.2015.01.054>

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Current Biology

Mantises Exchange Angular Momentum between Three Rotating Body Parts to Jump Precisely to Targets

Highlights

- Wingless mantises jump precisely to distant targets by juggling angular momentum
- At takeoff, they generate controlled whole-body spin by adjusting their COM
- Once airborne, they then adjust this spin by rotating three different body parts
- Restricting these body rotations results in crash landings or missing the target

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In Brief

Control of mid-air orientation is a complex problem faced by flightless animals. Here, Burrows et al. show that mantises fine-tune their targeted jumps by passing angular momentum between their rotating front legs, hind legs, and abdomen. These results have wider implications for biomechanical control and the development of jumping robots.



Mantises Exchange Angular Momentum between Three Rotating Body Parts to Jump Precisely to Targets

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Summary

Flightless animals have evolved diverse mechanisms to control their movements in air, whether falling with gravity or propelling against it. Many insects jump as a primary mode of locomotion and must therefore precisely control the large torques generated during takeoff. For example, to minimize spin (angular momentum of the body) at takeoff, plant-sucking bugs apply large equal and opposite torques from two propulsive legs [1]. Interacting gear wheels have evolved in some to give precise synchronization of these legs [2, 3]. Once airborne, as a result of either jumping or falling, further adjustments may be needed to control trajectory and orient the body for landing. Tails are used by geckos to control pitch [4, 5] and by *Anolis* lizards to alter direction [6, 7]. When falling, cats rotate their body [8], while aphids [9] and ants [10, 11] manipulate wind resistance against their legs and thorax. Falling is always downward, but targeted jumping must achieve many possible desired trajectories. We show that when making targeted jumps, juvenile wingless mantises first rotated their abdomen about the thorax to adjust the center of mass and thus regulate spin at takeoff. Once airborne, they then smoothly and sequentially transferred angular momentum in four stages between the jointed abdomen, the two raptorial front legs, and the two propulsive hind legs to produce a controlled jump with a precise landing. Experimentally impairing abdominal movements reduced the overall rotation so that the mantis either failed to grasp the target or crashed into it head first.

Results and Discussion

We analyzed videos of 381 targeted jumps performed by 58 juveniles of all larval stages of the mantis, *Stagmomantis theophila*. The target was a vertical, 4-mm diameter black rod placed against a white background at distances of 1–2 body lengths from the edge of a platform on which the mantis stood (Figure 1A; Movie S1). Juvenile stages superficially resemble adults, but because they do not have wings, they rely on targeted jumping to navigate between the twigs and leaves of their heterogeneous arboreal environment. The morphometrics of fifth, sixth, and seventh instar mantises and their jumping performance were analyzed (Table 1).

The form of the jump and the takeoff velocities were similar for each instar despite the 4-fold differences in mass. The following analysis focused on the sixth instar (three jumps by each of six individuals).

The first movements in preparation for a targeted jump were a sideways swaying of the head to scan the target and apparently determine its distance [12, 13]. The body then rocked backward, and the abdomen curled upward so that its tip pointed forward (Figure 1B). Propulsive forces were generated by depression of the proximal segments (trochantera and the closely linked femora) and extension of the more distal tibiae of the middle and hind legs. Thrust continued until both pairs of these legs were outstretched at takeoff. During this acceleration phase, which lasted for 33.8 ± 1.1 ms (mean of means), the abdomen was curled forward and upward, and the front legs were off the ground and were progressively rotated anticlockwise about the trunk to project in front of the body (Figure 1B; Supplemental Information; Movie S1). During these propulsive movements, the center of mass (COM) of the whole mantis (calculated from the sum of the COMs of individual body parts; see Supplemental Information) stayed on the longitudinal body axis (Figure 1C). Takeoff occurred at a velocity of 1.0 ± 0.1 m s⁻¹ (mean of means). The force from the legs was applied below the COM, resulting in an anticlockwise whole-body spin that set the appropriate body angle for a precise landing on the target.

To test that control of this directed takeoff was attributable to rotational movements of the front legs and abdomen about the trunk, we constructed a model based on the detailed data of a single natural jump by a sixth instar mantis. The COM was followed under three conditions: (1) natural jumps, (2) simulated jumps with the abdomen fixed in its starting position, and (3) simulated jumps with the front legs fixed in their starting positions. In these two simulations, other body parts were allowed to move in the same trajectory as recorded in the videos of natural jumping (Figure 1C). In the model, if movement of the abdomen was excluded, the COM fell ventrally from the longitudinal axis of the thorax and moved closer to the line of action of the propulsive legs, thus reducing the total spin of the body and altering its angle relative to the target. By contrast, excluding movements of the front legs in the second simulation did not shift the COM from the body.

Once airborne toward a target that was 1.5–2 body lengths distant, the sequence of leg and abdominal movements was the same from mantis to mantis. The COM moved around, but this had little effect on the trajectory because gravity always acts downward through the COM and thus generates no torque. The abdomen, front legs and hind legs performed a series of clockwise and anticlockwise rotations during which they exchanged angular momentum at different times and in different combinations. By contrast, the trunk underwent much smaller changes in its angular momentum, which were just sufficient to ensure that the mantis was oriented at the correct angle for landing on the vertical target. Air resistance [14] was calculated to exert a maximum spin of the body relative to the horizon of 5° (~20% of the total), making the exchange of angular momentum the dominant factor governing the rotation of the mantis. The four distinct exchanges of

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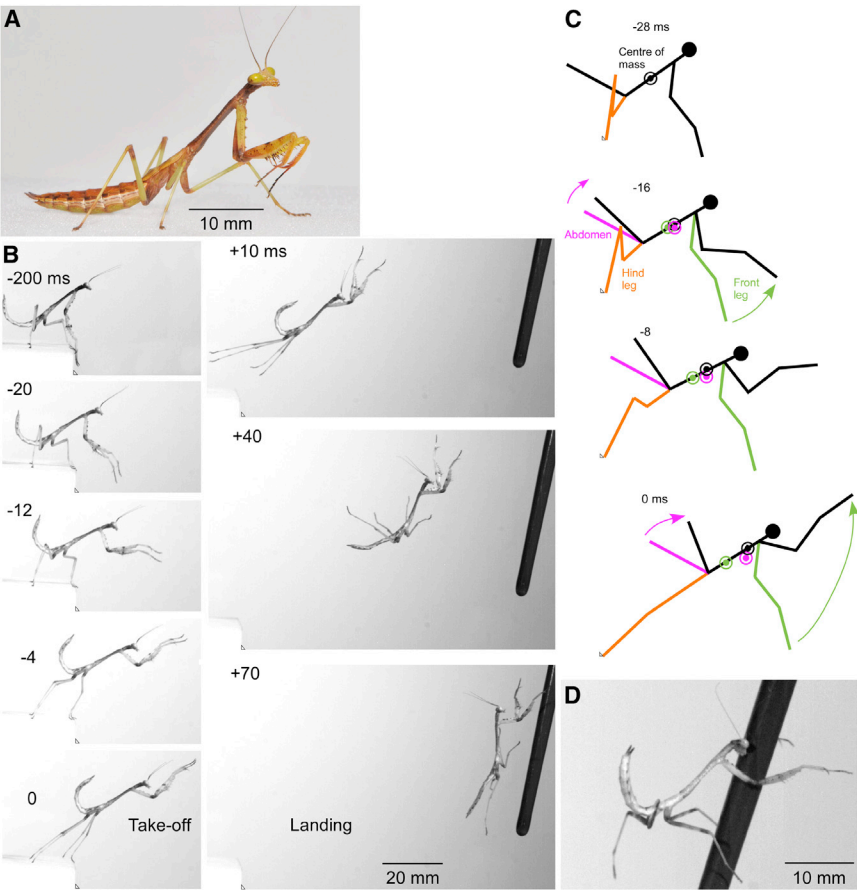


Figure 1. High-Speed Images of a Natural Jump (A) Photograph of a sixth instar mantis nymph. (B) Selected images from a natural jump by a sixth instar nymph captured at 1,000 frames s⁻¹. The open triangles indicate a constant reference point in all frames. Takeoff occurred at 0 ms, and the target was reached 70 ms later. During the airborne trajectory the abdomen, front and hind legs rotated about the thorax. (C) Stick diagrams of the changing positions of the trunk, abdomen, front legs (all black lines), and hind legs (orange lines) made by tracing individual frames at the times indicated during a natural jump. The arrows show the direction of rotation that would happen in a natural jump. The jump was then modeled with either the front legs (green) or the abdomen (pink) held constant in their starting positions but with the hind legs (orange) moving as they did in a natural jump. The resulting effect on the calculated COM is indicated by the colored circles: green and pink, respectively, for when the front legs or abdomen did not move. (D) Single frame from a jump by a fifth instar mantis in which the segments of the abdomen were glued together. The mantis did not rotate enough and hit the target with its head.

angular momentum between these components are detailed in the following example jump.

First (Figures 2A and 2B, I), during the initial 10 ms after takeoff, the front legs continued their upward and anticlockwise (positive) rotation and the hind legs their clockwise (negative) rotation about the trunk (head and thorax). For example, at 5 ms, the front legs had an angular momentum of 103 g mm² s⁻¹ and the hind legs -32 g mm² s⁻¹. The abdomen changed direction from its initial slow clockwise rotation about the trunk to a similarly slow anticlockwise rotation, giving it a negligible average angular momentum. The trunk had an angular momentum of 49 g mm² s⁻¹, giving a total angular momentum for the whole mantis of 139 g mm² s⁻¹. If the front legs had stopped rotating at this stage, then their angular momentum would have transferred to the trunk, resulting in a large increase in spin by the mantis from 0.6° to 2.3° ms⁻¹ relative to the horizontal.

Second, starting approximately 10 ms after takeoff, the rotation of the front legs came to a halt, while the anticlockwise rotation of the abdomen about the trunk increased. By 25 ms

into the jump, 103 g mm² s⁻¹ of angular momentum had been transferred from the front legs to the abdomen. The hind legs continued their clockwise rotation about the trunk with an angular momentum of -28 g mm² s⁻¹ (Figures 2A and 2B, II).

Third, a further 15 ms into the aerial trajectory and 40 ms after takeoff, the rotation of the hind legs was reversed to the anticlockwise direction, bringing them forward into their landing position with 10 g mm² s⁻¹ of momentum at 40 ms, rising to 97 g mm² s⁻¹ at 60 ms. This was synchronized with a deceleration of the abdominal rotation toward an angular momentum of 36 g mm² s⁻¹ at 60 ms and an opposing clockwise rotation of the front legs of approximately -29 g mm² s⁻¹ (Figures 2A and 2B, III). Again, opposing rotations, this time of the front and hind legs, maintained a low angular momentum of the trunk about the horizontal.

Last, during the final 10 ms before landing, the hind legs and abdomen stopped rotating. This was balanced by a sharp anticlockwise rotation of the front legs with 78 g mm² s⁻¹ of angular momentum (Figures 2A and 2B, IV). The net result of this entire sequence was that the trunk of the mantis spun by 50° relative to the horizontal with a near-constant angular momentum, aligning itself perfectly for landing with the front and hind legs ready to grasp the target.

Table 1. Jumping Parameters for Three Jumps by Each of Six Fifth, Six Sixth, and Six Seventh Instar Mantises Expressed as Mean of Means ± SEM

	Mass (mg)	Body Length (mm)	Front Leg Length (mm)	Middle Leg Length (mm)	Hind Leg Length (mm)	Takeoff Time (ms)	Body Angle at Takeoff (°)	Takeoff Angle (°)	Takeoff Velocity (m s ⁻¹)
Fifth instar	85.7 ± 6.9	30.5 ± 0.5	20.7 ± 0.6	15.7 ± 0.5	22.5 ± 0.5	30.0 ± 1.6	51.9 ± 2.1	45.6 ± 2.5	0.8 ± 0.1
Sixth instar	172.1 ± 17.4	39.7 ± 1.6	27.8 ± 1.3	20.8 ± 0.7	28.6 ± 1.6	33.8 ± 1.1	41.1 ± 1.5	38.0 ± 2.4	1.0 ± 0.1
Seventh instar	355.6 ± 35.6	44.4 ± 0.5	30.2 ± 0.8	21.1 ± 2.4	29.9 ± 1.4	37.7 ± 1.7	45.3 ± 2.8	38.2 ± 3.3	1.0 ± 0.1

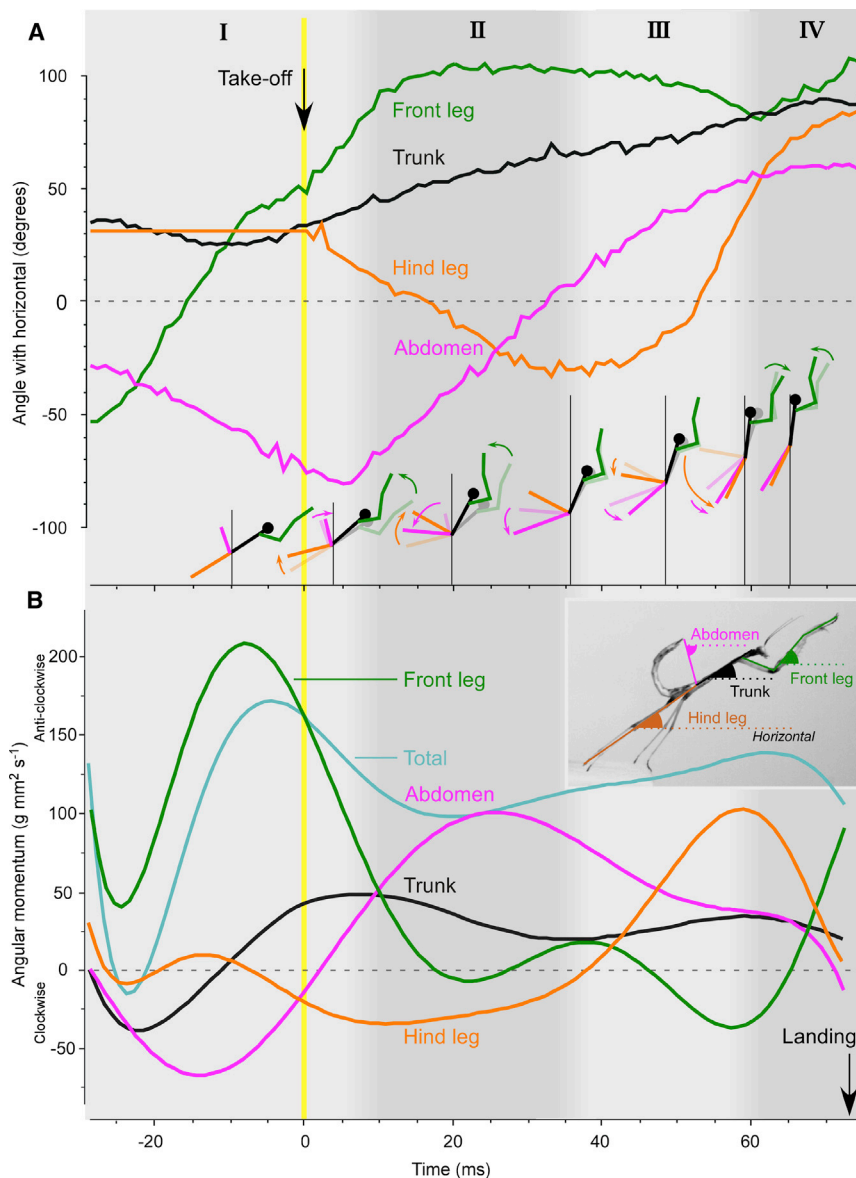


Figure 2. Kinematics and Modeling

(A) Changes in joint angles measured in each successive frame (1-ms intervals) from a video of a natural jump.

(B) Calculated changes in angular momentum of different body parts during the same jump. To produce continuous smooth curves of angular velocity, we measured the angles of the thorax, raptorial front legs, abdomen, and hind legs at each frame, fitted to ninth-order polynomials, which were then differentiated against time and used to generate curves of angular momentum (further details in [Supplemental Information](#)). The vertical shaded regions show the four periods (I–IV, demarcated by fuzzy boundaries) of the jump that are described in the text. The front legs (green), hind legs (orange), trunk (black), and abdomen (pink) are indicated. The total momentum of the mantis is shown in teal. The inset cartoon shows the angles measured relative to the horizontal. Takeoff occurred at 0 ms (yellow bar). The stick diagrams are tracings from frames of a video of the natural jump to show the orientations of the different body parts at the times indicated by the vertical black lines. The colored lines join the base of the body parts to their most distal points; the legs move in three dimensions, and the abdomen curves. The paler color shows the previous position of the body part, and the colored arrows show the direction of movement.

mantis now rotated 64% faster at $1.4^\circ \pm 0.2^\circ \text{ ms}^{-1}$ and spent 66% less time airborne ($44.9 \pm 3.8 \text{ ms}$) while still landing precisely on the target (mean of means for six sixth instar mantises each jumping three times, compared with 13 jumps by five mantises jumping to targets at 1.5–2 body lengths). The absence of leg and abdominal rotations here, accompanied by a higher rotation rate of the trunk, thus confirms a role for these rotations in reducing whole-body spin in the longer jumps and also suggests that they are under active muscular control.

To assess possible variability in this sequence, we analyzed in further detail 13 jumps by five sixth instar mantises to the vertical target 1.5–2 body lengths away. While airborne, the trunk rotated with an angular velocity of $0.9^\circ \pm 0.1^\circ \text{ ms}^{-1}$ (mean of means \pm SEM), and the abdomen and the hind legs rotated more than twice as fast at $2.9^\circ \pm 0.3^\circ \text{ ms}^{-1}$ and $2.3^\circ \pm 0.8^\circ \text{ ms}^{-1}$, respectively. The largest variability in angular velocity was thus seen in the rotations of the hind legs, where the SEM was approximately 25% of the mean compared to 10% for abdominal rotations. The time spent airborne for this group was $68.4 \pm 3.4 \text{ ms}$.

Two experimental manipulations were made to analyze the mechanics of the jump. First, the target distance was reduced, and the angular velocity of the trunk was measured. If the mantis is adjusting its rotations, then a shorter jump would have to be accompanied by a faster angular rotation of the trunk to align properly with the target. When jumping to a target one body length away, there were no anticlockwise rotations of the abdomen and the hind legs that occurred in periods II and III in jumps to the more distant targets (Figure 2). The

In the second manipulation, flexibility of the abdomen was reduced by supergluing the segments together, and this resulted in the mantises rotating at an angular velocity of $0.6^\circ \pm 0.2^\circ \text{ ms}^{-1}$ (mean of means of 17 jumps by two fifth instar mantises). This rate of rotation was 57% slower than that of unimpeded mantises when jumping the same distance of one body length. A further consequence was that the experimentally modified mantises did not rotate enough to land with the appropriate orientation to the target and thus failed to grasp it. Some under-rotations even resulted in mantises hitting the target headfirst before falling away from it (Figure 1D; [Supplemental Information](#); [Movie S2](#)).

What mechanisms do other animals use when making a targeted jump? Primates swing their front limbs forward, the mass of which is sufficient to act as a counterweight contributing to forward thrust [15, 16]. In the much lighter mantises, however, the swing of the front legs cannot contribute to thrust because of their small size [16, 17]. Other invertebrates stabilize their mid-air trajectories by altering aerodynamic drag, a very different mechanism that exploits air resistance

to maintain a constant orientation. Locusts curl their abdomen to help stabilize takeoff [18], and jumping spiders spin a drag line from their abdomen [19]. Some insects also use their hind legs as rudders when airborne [11, 20]. By contrast, while wind resistance increased the total angular momentum in the mantis, the rotation of the legs and abdomen kept the angular momentum of the trunk low (Figure 2B, compare teal and black lines). Conservation of angular momentum to achieve specific body orientations is exploited by lizards, the tails of which act as reservoirs of angular momentum [4–6], and by falling cats, which counter-rotate the front and hind parts of their bodies [8]. The mantis, however, uses four different exchanges of angular momentum between three different rotating and interacting body parts and, in doing so, reduces whole-body spin 3-fold toward a constant value commensurate with reaching and landing precisely on a target.

Some other insects (albeit ones that fly) have structures that they use as gyroscopes to provide fast sensory feedback during rotational motions. These operate over a timescale of milliseconds in flies (the halteres [21]) or tens of milliseconds in moths (the antennae [22]). Mantises do not have halteres, and their antennae are not large or mobile enough to match these feats. Moreover, while both halteres and antennae require Coriolis accelerations to measure angular velocity, mantises do not have structures that move in such a way as to generate and react to these forces (Movie S1). An assessment that now needs to be made for the mantis is the role of neural control (feedforward or feedback) in these exchanges of angular momentum. When jumping variable distances, mantises were able to adjust their rotation rates to achieve precise landings. Can the mantis also alter the trajectory of its jump after takeoff in response to changes in its environment? These principles of angular momentum exchange and their underlying control mechanisms could be extrapolated to the design of jumping robots, which presents a significant engineering problem to which solutions are still in the early stages of successful implementation [23–25]. The mechanism described here, like gears [3], screws [26], and high-speed lever systems [27], represents another natural prototype of man-made devices.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, one figure, one table, and two movies and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2015.01.054>.

Acknowledgments

G.P.S. was supported by HFSP grant LT00422/2006-C. D.A.C. was funded by a Leverhulme Trust grant F/09 364/K to S.R. Ott (University of Leicester), whom we thank for his support. We thank Alexis Braun for rearing the mantises and our colleagues for their suggestions on the draft manuscript.

Received: October 27, 2014

Revised: December 12, 2014

Accepted: January 22, 2015

Published: March 5, 2015

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